

# Climate variability and phytoplankton composition in the Pacific Ocean

Cecile S. Rousseaux<sup>1,2</sup> and Watson W. Gregg<sup>1</sup>

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[1] The effect of climate variability on the phytoplankton community was assessed for the tropical and sub-tropical Pacific Ocean between 1998 and 2007 using an established biogeochemical assimilation model. The tropical and sub-tropical phytoplankton communities exhibited a wide range of responses to climate variability, from radical shifts in the Equatorial Pacific, to changes of only a couple of phytoplankton groups in the North Central Pacific, to no significant changes in the South Pacific. In the Equatorial Pacific, climate variability represented by ENSO dominated the variability of phytoplankton. Here, nitrate, chlorophyll and all of the 4 phytoplankton types (diatoms, cyanobacteria, chlorophytes and coccolithophores) were strongly correlated ( $p < 0.05$ ) with the Multivariate El Niño Southern Oscillation Index (MEI). During La Niña events, diatoms increased and expanded westward along the cold tongue (correlation with MEI,  $r = -0.87$ ,  $p < 0.05$ ), while cyanobacteria concentrations decreased significantly ( $r = 0.69$ ,  $p < 0.05$ ). El Niño produced the reverse pattern, with cyanobacteria populations increasing while diatoms plummeted. In the North Central Pacific, the MEI was significantly correlated with diatoms ( $r = -0.40$ ) and chlorophytes ( $r = -0.43$ ). Ocean biology in the South Pacific was not significantly correlated with MEI. The phytoplankton composition from the assimilation model was compared to that from a new empirical algorithm using satellite data. Despite differences in the absolute concentration, the relative abundance from the model and the satellite-derived approach showed a similar shift in phytoplankton community in the Equatorial Pacific. These results highlight the spatially variable nature of the relationship between phytoplankton community structure and climate variability within the Pacific Ocean.

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## 1. Introduction

[2] The El Niño Southern Oscillation (ENSO) is the dominant source of interannual climate variability in the tropical Pacific Ocean. During the 1997–98 El Niño event, one of the strongest ENSO events observed by Ocean Color data, the phytoplankton concentration, represented by chlorophyll, decreased in the Equatorial Pacific [e.g., Behrenfeld *et al.*, 2006; Boyce *et al.*, 2010; Martinez *et al.*, 2009; Strutton and Chavez, 2000] and the associated Peruvian anchovy fishery collapsed [Chavez *et al.*, 2003]. The generalized mechanisms for these events are well described: wind reversal during El Niño leads to reduced upwelling in the eastern tropical Pacific, impacting total phytoplankton

concentration and the fisheries that depend upon them. However, the effect climate variability has on phytoplankton community structure is less well known, as is the spatial and temporal extent of the effects. Based on historical data sets, there are some indications that climate variability may shift the phytoplankton community structure [Bidigare and Ondrusek, 1996; Karl *et al.*, 2001]. The effects of these climate variability events on phytoplankton community structure at a global scale are only now beginning to be explored [Bricaud *et al.*, 2012; Masotti *et al.*, 2011; Uitz *et al.*, 2010]. Satellite algorithms for identifying phytoplankton taxonomic distributions are just now emerging (for a review, see Brewin *et al.* [2011]).

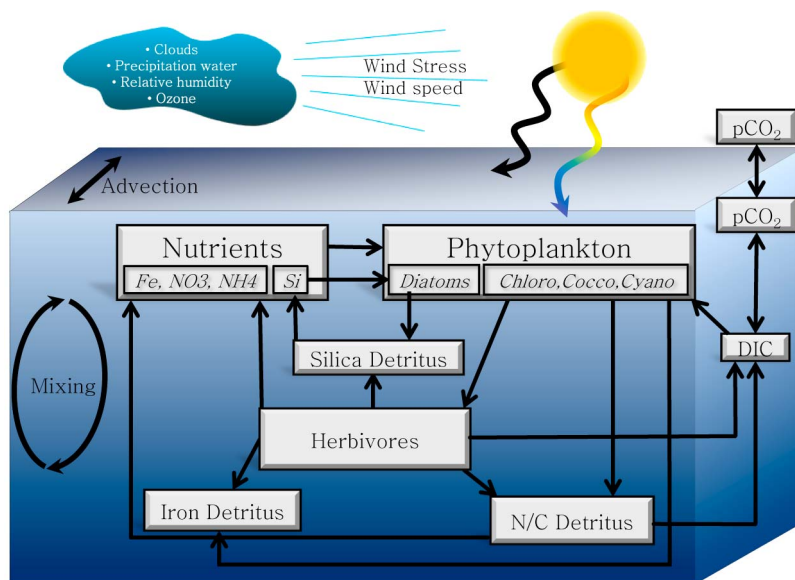
[3] Each phytoplankton taxon thrives under specific physical and chemical conditions and have their own biogeochemical functionality. Diatoms, for example, require the presence of nutrient-rich conditions and support a relatively short food chain that leads from phytoplankton to zooplankton to fish [Cushing, 1989]. On the other extreme, cyanobacteria can survive in low nutrient conditions and support a food-web that relies more heavily upon recycled nutrients, has a high turnover, and where bacteria and pico-phytoplankton are consumed by protozoa, ciliates and

<sup>1</sup>Global Modeling and Assimilation Office, NASA Goddard Space Flight Center, Greenbelt, Maryland, USA.

<sup>2</sup>Universities Space Research Association, Columbia, Maryland, USA.

Corresponding author: C. S. Rousseaux, Global Modeling and Assimilation Office, NASA Goddard Space Flight Center, Bldg. 33, G105, Greenbelt Rd., Greenbelt, MD 20771, USA. (cecile.s.rousseau@nasa.gov)

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**Figure 1.** Schematic representation of the NOBM. Interactions among the main components of NOBM, nominal input and forcing fields. The model comprises four phytoplankton groups (Diatoms, Chlorophytes, Coccolithophores and Cyanobacteria), four nutrient groups (Iron, Nitrate, Ammonium and Silica), a single herbivore group and three detrital components (Iron, Silica and Nitrogen/Carbon). Carbon cycling involves dissolved inorganic carbon (DIC), dissolved organic carbon (not represented here) and  $p\text{CO}_2$ . Radiative transfer calculations provide the underwater irradiance fields necessary to drive phytoplankton growth, and interact with the heat budget. It requires external monthly climatologies of cloud properties, surface pressure, wind speeds, relative humidity, precipitable water, and ozone (see Gregg [2008] for more details).

microzooplankton [Azam *et al.*, 1983; Cushing, 1989]. Between these two extremes, a multitude of phytoplankton groups exist with a wide variety of responses to environmental changes.

[4] The knowledge we have on the effect climate variability has on these different phytoplankton groups is limited. Most historical data sets have been collected in the Equatorial Pacific and in the eastern North Central Pacific. Because of the spatial and temporal heterogeneity of in situ data sets, the spatial and temporal extent large-scale climatic events such as El Niño and La Niña may have on the individual phytoplankton taxa remains unclear. Numerical models have the advantage to include many of the complex interactions necessary to describe responses to climate variability and provide estimates of the distribution of phytoplankton groups in a mechanistic and consistent manner. When assimilating satellite data, these models additionally provide improved estimates of the total chlorophyll field and the changes associated with climate variability. Here, we use an established data assimilation model to investigate the spatial and temporal extent climatic variability has on the phytoplankton composition in the Pacific Ocean.

[5] Recently, a variety of bio-optical methods have been established that use satellite data to identify and differentiate between phytoplankton functional types (PFTs) and sizes in the surface ocean. Some of these approaches were inter-compared in the review paper of Brewin *et al.* [2011] and new methods are frequently being developed and improved [e.g., Kostadinov *et al.*, 2009, 2010; Mouw and Yoder, 2010]. Hirata *et al.* [2011] developed an empirical algorithm to estimate the fractional contribution of seven phytoplankton functional types partitioned within three size classes. Here we

compare our results with those from this new algorithm. The Hirata *et al.* [2011] satellite-derived approach was chosen for comparison here because (1) it estimates the phytoplankton composition at a global scale, (2) it allows the derivation of absolute abundance (and not dominance) and (3) it allows the estimation of PFTs enabling sufficient compatibility with the taxonomic definition of the assimilation model to facilitate a meaningful intercomparison.

## 2. Material and Methods

[6] The NASA Ocean Biogeochemical Model (NOBM) is a biogeochemical model of the global oceans that is coupled with a circulation and radiative model [Gregg and Casey, 2007] (Figure 1). The model has been extensively validated [Gregg and Casey, 2007; Gregg *et al.*, 2003], involving a comparison of 9 of the 14 model state variables against in situ and/or satellite data sets (only herbivores, the 3 detrital components, and dissolved organic carbon have not been validated). The model contains 4 explicit phytoplankton taxonomic groups: diatoms, cyanobacteria, chlorophytes, and coccolithophores, to represent the large scale biodiversity of the global oceans. In the model, the diatoms and cyanobacteria represent functional extremes, as described above. The chlorophytes represent an intermediate group, occupying the transitional regions between the high nutrients regions dominated by diatoms and the nutrient-scarce regions dominated by cyanobacteria. The coccolithophores have an ability to tolerate lower nutrient conditions than diatoms and chlorophytes, but not as low as cyanobacteria, but have the property of sinking faster than most phytoplankton during periods of high growth.

**Table 1.** Percentage Difference in Relative Abundance Between the Model and the in Situ Data<sup>a</sup>

|                  | North Central Pacific | Equatorial Pacific | South Pacific |
|------------------|-----------------------|--------------------|---------------|
| Diatoms          | −3.50 (3)             | −0.87 (21)         | 25.58 (7)     |
| Chlorophytes     | −19.40 (2)            | −18.01 (17)        | −33.32 (7)    |
| Cyanobacteria    | 10.67 (24)            | −13.47 (20)        | 3.20 (2)      |
| Coccolithophores | 1.99 (3)              | 36.77 (15)         | −2.11 (7)     |

<sup>a</sup>The number of observations used for the comparison is given in parentheses.

[7] As with nutrients and total chlorophyll, the phytoplankton groups in the model have been validated against in situ data [Gregg and Casey, 2007] (publicly available at the Global Modeling and Assimilation Office (GMAO) web site, gmao.gsfc.nasa.gov). This data set includes 469 surface-layer observations of phytoplankton group abundances (full list of references available in Gregg and Casey [2007]). The data are converted when necessary into percent abundance of the entire population to compare with the model. In our validation, we match up model mixed-layer relative abundances with the location and month of the in situ observations. We assemble all of these co-located, coincident match-ups over ocean basins, and over all the months for a year. We then average these match-ups over the basin annually. This provides us an opportunity to observe the large scale spatial performance of the model while keeping a close model-data relationship. We perform a correlation analysis using these annual means across the basins to evaluate correspondence of distributions on basin scales. The difference is expressed as model minus observations. Three (cyanobacteria, diatoms and coccolithophores) of the four phytoplankton groups exhibit statistically significant correlation between model and observations ( $p < 0.05$ ) across the major global oceanographic basins (Table 1). The lack of statistical significance for the chlorophytes is derived from their absence in the model in the Antarctic and sub-polar North Pacific, which is not of interest in this effort. For the sub-tropical and tropical Pacific basins studied here, the phytoplankton relative abundances are always within 37% (absolute difference in relative abundance) of the in situ data set in the 12 possible cases (4 phytoplankton groups in 3 oceanographic basins). Only 3 cases are  $>20\%$  (Table 1): a nearly  $\sim 33\%$  underestimate of model chlorophytes in the South Pacific, a 25% model overestimate of diatoms in the South Pacific, and a 37% model overestimate of coccolithophores in the Equatorial Pacific. Note that in this paper, when referring to the term ‘abundance’ we refer specifically to chlorophyll abundance.

[8] Total chlorophyll fields (sum of all phytoplankton components) in NOBM are assimilated using Sea-viewing Wide Field-of-view Sensor (SeaWiFS) data from 1998 to 2007. The assimilation produces chlorophyll estimates within 0.1% bias and 33.4% uncertainty as compared to in situ data [Gregg, 2008], similar statistically to SeaWiFS and in situ data. Phytoplankton relative abundances are not directly affected by the data assimilation, but they can be affected indirectly via changes in concentration gradients, light availability, and nutrient availability that are derived from changes in total chlorophyll. An enhancement to the assimilation model is the online correction of nutrient fields corresponding to the assimilated satellite chlorophyll data.

[9] The assimilation of chlorophyll by nature changes the balance between the chlorophyll-containing phytoplankton and the nutrients needed to support them. Most of the time the imbalance is small and is corrected by the interaction of the physics and biology in the model. However, sometimes this imbalance can be important, especially in regions where the chlorophyll assimilation is a persistent adjustment to a persistent model bias. This is observed in the South Pacific where the model produces higher chlorophyll than the satellite observes, and there is high concentration of nitrate in the deep waters. The assimilation of chlorophyll reduces the concentrations, resulting in reduced nitrate uptake, and leading to excessive nitrate arising from deep water to the surface layer (auxiliary material Figure S1).<sup>1</sup> In a multivariate assimilation methodology, these imbalances derived from the assimilation of satellite chlorophyll are corrected using a mechanistic approach involving the nutrient-to chlorophyll ratios embedded in the model. The difference between the chlorophyll assimilation results and the prior chlorophyll produced by the model (the analysis increments) are used to adjust the nutrient concentrations. The multivariate assimilation is applied to silica and dissolved iron, as well as nitrate. The results are shown in Figure S1, where the multivariate nutrient assimilation is compared to the uni-variate assimilation and free-run model where no assimilation occurs and the concentrations are balanced by the enforcement of model equations. Details on the multivariate assimilation of nutrients can be found in Appendix 1 in Text S1.

[10] To understand the effects of climate variability on phytoplankton composition at a global scale, we divide the Pacific Ocean into 3 major oceanographic basins (North Central, Equatorial and South Pacific Ocean) to cover both the tropical Pacific where most of the ENSO effect occurs, and the sub-tropical regions. The Equatorial Pacific extends between  $10^{\circ}\text{S}$  and  $10^{\circ}\text{N}$ , the North Central Pacific from  $10^{\circ}\text{N}$  to  $40^{\circ}\text{N}$  and the South Pacific Ocean from  $10^{\circ}\text{S}$  to  $40^{\circ}\text{S}$ . Linear trends and seasonal climatology are removed to highlight the inter-annual variability which is the emphasis here. The seasonal mean is added back to produce representative chlorophyll concentrations as opposed to anomalies. Seasons are defined as four 3-month segments beginning in January.

[11] The link between biology and the physical oscillation of the tropical and sub-tropical Pacific Ocean is quantified by the correlation coefficient found between the Multivariate El Niño Southern Oscillation Index (MEI) and biochemical output from the assimilated NOBM. The MEI attempts to characterize climate variability using six relevant atmospheric and ocean variables (sea level pressure, surface wind vector, sea surface temperature, surface air temperature, and total cloudiness fraction [Wolter and Timlin, 1998]). The MEI has been widely used in assessing the effect of climate variability on ocean biology [e.g., Behrenfeld et al., 2006; Dave and Lozier, 2010; Kostadinov et al., 2010; Matsumoto and Furuya, 2011; Villanoy et al., 2011]. In this paper when referring to climate variability we refer specifically to MEI. We test an additional 10 climate indices to evaluate the robustness of our results (see Appendix 2 in Text S1). The MEI is positive in El Niño phase and negative

<sup>1</sup>Auxiliary materials are available in the HTML. doi:10.1029/2012JC008083.

**Table 2.** Correlation Coefficient for the Climate Index and Biological Data in North Central Pacific Ocean, Equatorial Pacific and South Pacific Ocean<sup>a</sup>

|                              | MEI          | Nitrate      | Diatoms      | Chlorophytes | Cyanobacteria | Coccolithophores |
|------------------------------|--------------|--------------|--------------|--------------|---------------|------------------|
| <i>North Central Pacific</i> |              |              |              |              |               |                  |
| MEI                          | 1.00         | -            | -            | -            | -             | -                |
| Nitrate                      | 0.17         | 1.00         | -            | -            | -             | -                |
| Diatoms                      | <b>-0.40</b> | <b>0.42</b>  | 1.00         | -            | -             | -                |
| Chlorophytes                 | <b>-0.43</b> | -0.26        | -0.01        | 1.00         | -             | -                |
| Cyanobacteria                | 0.17         | -0.15        | <b>-0.38</b> | -0.02        | 1.00          | -                |
| Coccolithophores             | -0.14        | -0.10        | -0.03        | 0.24         | 0.03          | 1.00             |
| Total Chlorophyll            | <b>-0.50</b> | 0.00         | <b>0.44</b>  | <b>0.67</b>  | 0.25          | <b>0.50</b>      |
| <i>Equatorial Pacific</i>    |              |              |              |              |               |                  |
| MEI                          | 1.00         | -            | -            | -            | -             | -                |
| Nitrate                      | <b>-0.71</b> | 1.00         | -            | -            | -             | -                |
| Diatoms                      | <b>-0.87</b> | <b>0.91</b>  | 1.00         | -            | -             | -                |
| Chlorophytes                 | <b>-0.39</b> | <b>0.43</b>  | 0.29         | 1.00         | -             | -                |
| Cyanobacteria                | <b>0.69</b>  | <b>-0.88</b> | <b>-0.81</b> | <b>-0.46</b> | 1.00          | -                |
| Coccolithophores             | <b>0.33</b>  | <b>-0.60</b> | <b>-0.53</b> | <b>-0.42</b> | <b>0.57</b>   | 1.00             |
| Total Chlorophyll            | <b>-0.89</b> | <b>0.77</b>  | <b>0.89</b>  | <b>0.44</b>  | <b>-0.63</b>  | -0.22            |
| <i>South Pacific</i>         |              |              |              |              |               |                  |
| MEI                          | 1.00         | -            | -            | -            | -             | -                |
| Nitrate                      | 0.19         | 1.00         | -            | -            | -             | -                |
| Diatoms                      | 0.18         | <b>0.73</b>  | 1.00         | -            | -             | -                |
| Chlorophytes                 | 0.08         | 0.18         | 0.22         | 1.00         | -             | -                |
| Cyanobacteria                | -0.15        | <b>-0.49</b> | <b>-0.66</b> | <b>-0.49</b> | 1.00          | -                |
| Coccolithophores             | -0.01        | -0.06        | -0.14        | -0.03        | <b>0.33</b>   | 1.00             |
| Total Chlorophyll            | 0.10         | <b>0.43</b>  | <b>0.56</b>  | <b>0.64</b>  | -0.21         | <b>0.42</b>      |

<sup>a</sup>Bold indicates  $p < 0.05$ .

in La Niña and is obtained from NOAA Earth Systems Research Laboratory (ESRL: [www.esrl.noaa.gov](http://www.esrl.noaa.gov)).

[12] Although the model contains explicit state representations of 4 nutrients, nitrate, ammonia, silica, and dissolved iron, we emphasize the relationships between nitrate and the chlorophyll and phytoplankton components, since during ENSO events, the distributions of other nutrients are dominated by the effects of upwelling and they respond similarly to nitrate.

[13] The phytoplankton composition derived from the NOBM is compared to an empirical satellite algorithm developed by *Hirata et al.* [2011]. This algorithm is based on empirical relationships between chlorophyll and PFTs (and size classes). *Hirata et al.* [2011] quantified the relationship between satellite derived chlorophyll and HPLC data using a least squares fitting approach. This algorithm allows the estimate of 3 phytoplankton size classes (micro-, nano- and pico-plankton) and 7 phytoplankton ‘functional’ types (diatoms, prymnesiophytes, green algae, dinoflagellates, prokaryote, picoeukaryote and *Prochlorococcus* sp.). The phytoplankton groups of *Hirata et al.* [2011] do not map directly onto the classifications of NOBM. Diatoms and green algae of *Hirata et al.* [2011] correspond closely with diatoms and chlorophytes of NOBM. There is a looser association, but still functionally representative, between picoplankton in *Hirata et al.* [2011] and the cyanobacteria of NOBM. The *Hirata et al.* [2011] classification of prymnesiophytes is much broader and encompasses more phytoplankton types than any representation in NOBM, but is closest generally to coccolithophores. Acknowledging the differences in classification, we proceed to make statistical comparisons. Hereafter, we refer to these groups as diatoms, chlorophytes, cyanobacteria and coccolithophores whether we discuss NOBM or the satellite-derived approach. Linear trends and seasonal

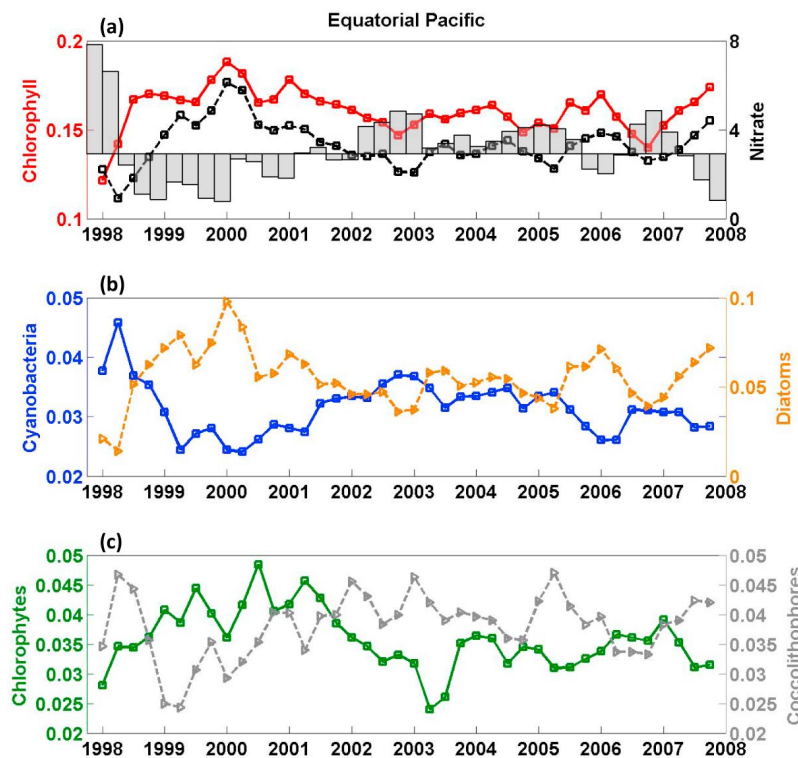
climatology are removed in the satellite-derived data set in the same way as for the NOBM results.

[14] To illustrate the independency of the two approaches, and therefore the validity of our comparison between satellite and model-derived phytoplankton composition, we compare the relative abundance of the four phytoplankton groups between the free-run and the assimilation. We find that the absolute difference in relative abundance was always less than 5% except in the Equatorial Pacific for cyanobacteria (~8% increase in relative abundance after assimilation) and diatoms (~5% decrease in relative abundance after assimilation) and in the South Pacific for chlorophytes (~5% decrease after assimilation).

### 3. Results and Discussion

#### 3.1. Temporal Patterns in Phytoplankton Related to Climate Variability Derived From the NOBM

[15] The link between biology and the physical environment related to climate variability was most evident in the Equatorial Pacific: nitrate, total chlorophyll, and every phytoplankton group was strongly correlated with MEI ( $p < 0.05$ ) (Table 2). The inverse relationship between MEI and nitrate ( $r = -0.71$ ) indicated depletion during El Niño. Subsequent declines in total chlorophyll, driven mostly by the reduction in diatoms, also exhibited a strong negative correlation. The negative correlation between cyanobacteria and nitrate ( $r = -0.88$ ) and coccolithophores and nitrate ( $r = -0.60$ ), were consistent with their abilities to survive in low nutrients [*Eppley et al.*, 1969; *Gregg and Casey*, 2007]. The time sequence of the MEI, nitrate, and phytoplankton indicated the evolution of the interannual variability and the different responses of phytoplankton and nitrate (Figure 2). The start of 1998 (El Niño conditions) was characterized by



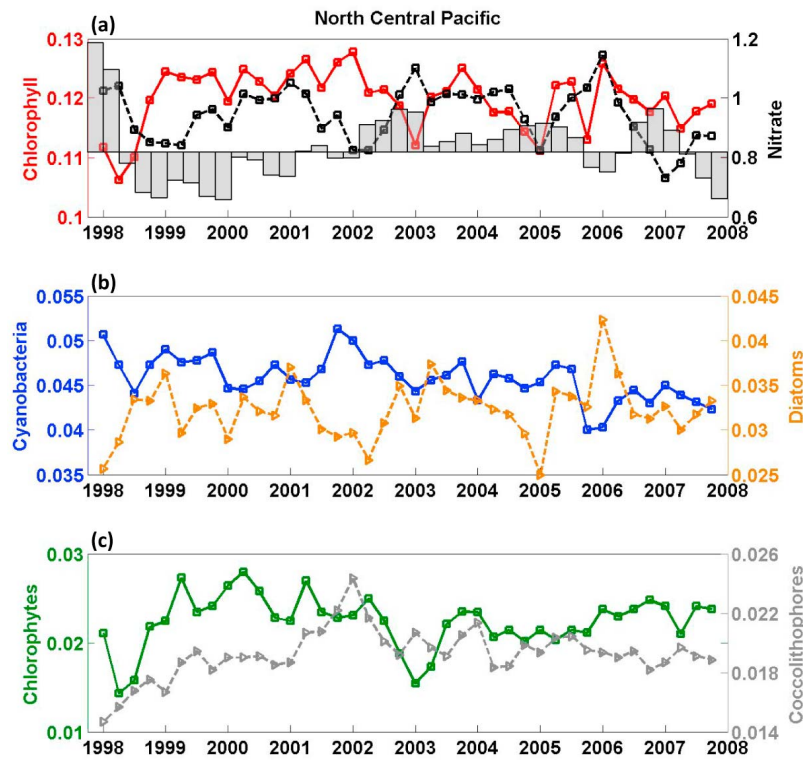
**Figure 2.** Temporal variation of nitrate and phytoplankton concentration in the Equatorial Pacific. Seasonal average (JFM, detrended, seasonal climatology removed and average added) of (a) chlorophyll  $a$  ( $\text{mg chl } a \text{ m}^{-3}$ ) and nitrate concentration ( $\mu\text{M}$ ). Shaded bars represent the MEI, note that the MEI was scaled to fit the plot (MEI varied between  $-1.33$  and  $2.68$  over the period 1998–2007). (b) Abundance of cyanobacteria and diatoms from NOBM ( $\text{mg chl } a \text{ m}^{-3}$ ). (c) Abundance of chlorophytes and coccolithophores from NOBM ( $\text{mg chl } a \text{ m}^{-3}$ ).

low nitrate and the chlorophyll concentration was the lowest observed over the period 1998–2007. At the same time, cyanobacteria reached their maximum concentration as diatom concentrations reached their lowest value. As La Niña conditions intensified in late 1998, nitrate concentration increased and produced a phytoplankton succession sequence. Diatoms were the first group to respond to the nutrient input. Diatoms responded to the input of nitrate by a  $\sim$ fourfold increase in their concentration (from  $\sim 0.021 \text{ mg chl } a \text{ m}^{-3}$  at the start of 1998 to  $\sim 0.072 \text{ mg chl } a \text{ m}^{-3}$  at the start of 1999). Chlorophyte concentration followed a similar temporal variability as diatoms. In the first half of 2000, the MEI increased, from  $-1.2$  to  $-0.1$  (i.e., toward more normal conditions), and nitrate concentration dropped. Although these conditions led to a decrease in diatoms, coccolithophores and chlorophytes appeared to benefit from this return to ‘normal’ conditions. In the Equatorial Pacific, the link between MEI and the phytoplankton community structure was through the fluctuation in nitrate concentration.

[16] We note that the phytoplankton composition in the model used is not being forced toward a particular state but rather responds to climatic fluctuations that are embedded in the atmospheric data used for forcing. The output from the model agreed with the historical observations of the effects El Niño and La Niña events have on the phytoplankton community in the Pacific Ocean. Previous studies based on in situ data [e.g., Bidigare and Ondrusek, 1996; Karl *et al.*, 2001]

and satellite observations [Bricaud *et al.*, 2012; Masotti *et al.*, 2011; Uitz *et al.*, 2010] have suggested a switch from a phytoplankton community dominated by picoplankton (functionally the equivalent of cyanobacteria here) during El Niño to a community dominated by diatoms during La Niña events. Using a biogeochemical model, we were able to quantify the details of the shift, its spatial and temporal extent, and the correlations between nutrients and among the phytoplankton taxa.

[17] In contrast to the Equatorial Pacific, the relationship between MEI and phytoplankton composition was more subtle in the North Central Pacific (Table 2 and Figure 3) and nonexistent in the South Pacific (Table 2 and Figure 4). The North Central Pacific is a biogeographically diverse basin, with a large central gyre bounded by regions of modest to large productivity at the lateral and northern margins. There is no feature like the upwelling cold tongue in the Equatorial Pacific that is strongly influenced by climate variability. The response of phytoplankton community composition to climate variability was mixed (Figure 3 and Table 2). MEI was no longer significantly correlated to nitrate. Although increasing nitrate concentration coincided with increasing diatom concentration ( $r = 0.42$ ), there was not a clear phytoplankton succession as occurred in the Equatorial Pacific. The MEI was only significantly correlated to diatoms ( $r = -0.40$ ) and chlorophytes ( $r = -0.43$ ) in this region.



**Figure 3.** Temporal variation of nitrate and phytoplankton concentration in the North Central Pacific. Seasonal average (JFM, detrended, seasonal climatology removed and average added) of (a) chlorophyll *a* ( $\text{mg chl } a \text{ m}^{-3}$ ) and nitrate concentration ( $\mu\text{M}$ ). Shaded bars represent the MEI, note that the MEI was scaled to fit the plot (MEI varied between  $-1.33$  and  $2.68$  over the period 1998–2007). (b) Abundance of cyanobacteria and diatoms from NOBM ( $\text{mg chl } a \text{ m}^{-3}$ ). (c) Abundance of chlorophytes and coccolithophores from NOBM ( $\text{mg chl } a \text{ m}^{-3}$ ).

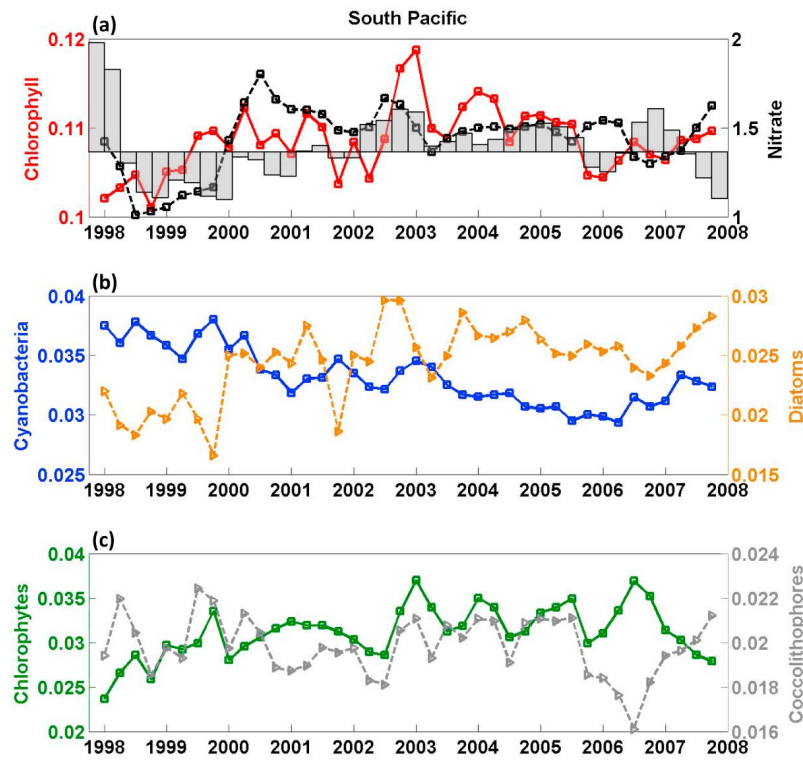
[18] The South Pacific is dominated spatially by a vast gyre, where nutrients are limited and cyanobacteria dominate. MEI was not correlated with nitrate nor was it correlated with chlorophyll concentration or any of the phytoplankton groups (Figure 4 and Table 2). The South Pacific was nearly impervious to the interannual climate variability investigated here. Although there was some evidence of a decrease in nitrate and total chlorophyll at the 1998 transition, the change in chlorophyll was small (note the scale) and the response was short-lived, as subsequent smaller ENSO events exhibited no statistical correlation. The only effects of climate variability occurred at the margins of the basins, near land features, where upwelling and mixing provided enough nutrients to modify the populations and distributions of eukaryotic phytoplankton, and then the resulting distributions of cyanobacteria.

### 3.2. Spatial Patterns in Phytoplankton Related to Climate Variability Derived From the NOBM

[19] Spatially, the effect of climate variability on phytoplankton community composition showed radical shifts, as shown in an idealized conceptual diagram derived from the results (Figure 5 derived from spatial distributions of phytoplankton concentrations provided in Figures 6 and 7). The spatial pattern shifts were especially notable for the phytoplankton functional extremes, diatoms and cyanobacteria. During El Niño events, when nutrients were limited,

cyanobacteria were predominant in the tropical Pacific Ocean (Figures 5 and 6). Diatoms, in contrast, were restricted to the eastern portion of the Equatorial Pacific. During La Niña events, when the upwelling was restored and nutrients replenished, diatoms expanded westward to the date line along the cold tongue while cyanobacteria retreated to the gyres and the extreme western portion of the tropical Pacific. This produced a significant inverse relationship between diatoms and cyanobacteria ( $r = -0.81$ , Table 2).

[20] The distribution of the two other phytoplankton groups of interest, chlorophytes and coccolithophores, also varied with climate variability although to a lesser extent when compared to diatoms and cyanobacteria (Figures 5 and 7). During La Niña, chlorophytes were distributed to the immediate north and south of the equatorial cold tongue and coccolithophores occupied the western edge. In the North Central Pacific, the significant relationship between MEI and chlorophytes ( $r = -0.43$ ) was due to an increase in chlorophytes during La Niña locally along the coast of Mexico and extending westward. Chlorophytes have been characterized as occupying transitional regions [Ondrusek *et al.*, 1991]. In the model, they inhabited areas where nutrients and light availability were insufficient to allow diatoms to predominate, but not in areas where nutrients were so low as to prevent losses by sinking to compensate growth. In the South Pacific, the area where chlorophytes predominated was similar (near the Chilean coast), during

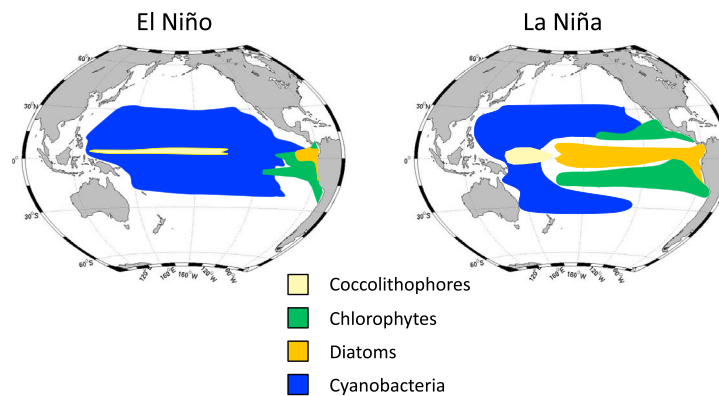


**Figure 4.** Temporal variation of nitrate and phytoplankton concentration in the South Pacific. Seasonal average (JFM, detrended, seasonal climatology removed and average added) of (a) chlorophyll *a* ( $\text{mg chl } a \text{ m}^{-3}$ ) and nitrate concentration ( $\mu\text{M}$ ). Shaded bars represent the MEI, note that the MEI was scaled to fit the plot (MEI varied between  $-1.33$  and  $2.68$  over the period 1998–2007). (b) Abundance of cyanobacteria and diatoms from NOBM ( $\text{mg chl } a \text{ m}^{-3}$ ). (c) Abundance of chlorophytes and coccolithophores from NOBM ( $\text{mg chl } a \text{ m}^{-3}$ ).

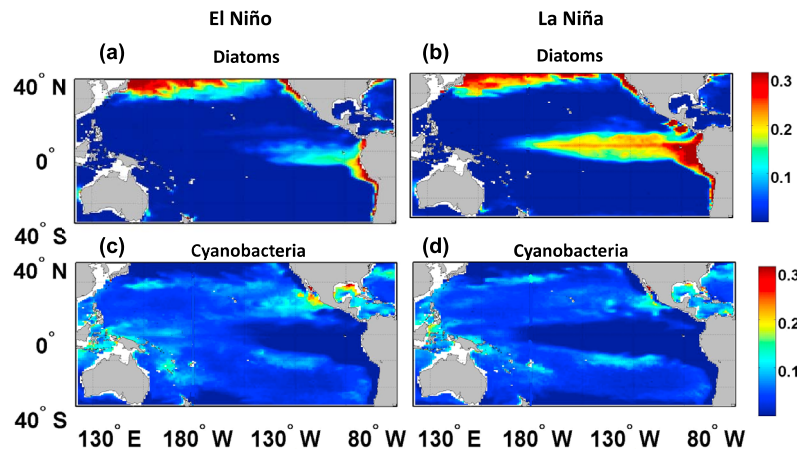
both El Niño and La Niña events, corroborating the statistical results that this region is relatively insensitive to climate variability.

[21] During La Niña events, coccolithophores occupied the western edge of the cold tongue (Figures 5 and 7). During

El Niño, coccolithophores expanded eastward along a narrow band in the Equatorial Pacific. In the model, the eastern Equatorial Pacific was where nutrients begin to become depleted, therefore giving way to coccolithophores because of their ability to grow in areas where nutrients and light were



**Figure 5.** Conceptual description of the effect climate variability has on the distribution of phytoplankton community structure in the Pacific Ocean (derived from the spatial distribution of phytoplankton concentration provided in Figures 6 and 7). An average for JFM 1998 was used as representative of El Niño conditions and an average for JFM 2000 was used as for La Niña. The spatial patterns loosely approximate predominance, except for coccolithophores where presence is depicted because they are rarely predominant.

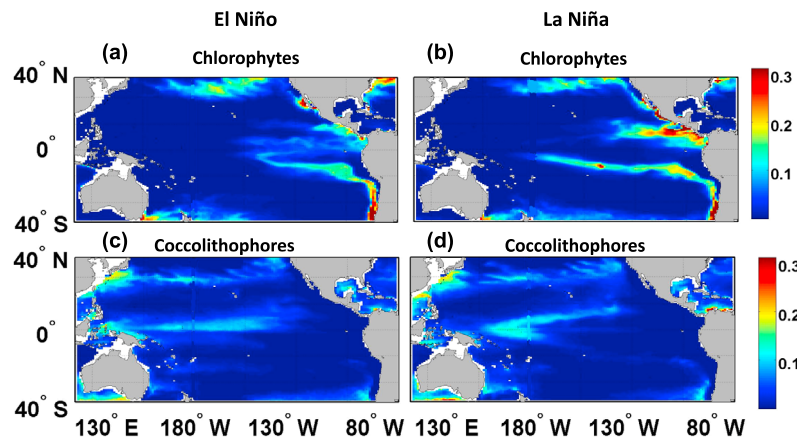


**Figure 6.** Effects of climate variability on the functional extreme derived from NOBM. Average (a, b) diatoms and (c, d) cyanobacteria concentration ( $\text{mg chl } a \text{ m}^{-3}$ ) during El Niño (January–March 1998) and La Niña events (January–March 2000) in the Pacific Ocean.

low enough to inhibit growth by diatoms and chlorophytes, but where there was insufficient vertical mixing to prevent their sinking losses, or where they could find nutrients at depth under low illumination levels. *DiTullio et al.* [2003] reported negligible abundances in the western Equatorial Pacific and *Ishizaka et al.* [1997] found also low ( $<10\%$ ) relative abundances here. Conversely, it is established that coccolithophores are present in the western Equatorial Pacific [*Higgins and Mackey*, 2000; *Ishizaka et al.*, 1997] sometimes in moderate relative abundances up to 35% of the total population, and containing very diverse assemblages of species [*Hagino et al.*, 2000; *Okada and Honjo*, 1973]. The abundance of coccolithophores has also been reported to be lowest during El Niño events compared to non El Niño events in the western Pacific ( $175^\circ\text{E}$  [*Ishizaka et al.*, 1997]). Comparison of our data assimilation results for 11 unique data locations in the western Equatorial Pacific showed mean relative abundance of 32.3% compared to 25.8% observed.

### 3.3. Intercomparison of Model- and Satellite-Derived Phytoplankton Community Composition

[22] Error characterization of the model and satellite-derived approaches have been independently estimated using different evaluation data sets. Comparing both to the same data set provided new information on the performance of the different methods in a common framework. Phytoplankton group relative abundances estimated from the satellite-derived approach were closer to the in situ data than NOBM in 8 out of the 12 cases (Table 3). Satellite-derived phytoplankton composition was always within 18% of in situ data except in one case where the satellite-derived approach underestimated chlorophytes by  $\sim 39\%$  in the South Pacific. However, the two methods tended to miss the in situ data in the same way. In all but three cases the difference between the satellite-derived phytoplankton and in situ data, and the NOBM difference were within 10% of one another (Tables 1 and 3). This suggested commonality between the representations of phytoplankton spatially in the Pacific Ocean. As indicated by *Hirata et al.* [2011], the largest uncertainty of their



**Figure 7.** Effect of climate variability on transitional groups derived from NOBM. Average (a, b) chlorophytes and (c, d) coccolithophores concentration ( $\text{mg chl } a \text{ m}^{-3}$ ) during El Niño (January–March 1998) and La Niña events (January–March 2000) in the Pacific Ocean.

**Table 3.** Percentage Difference Between the Method of *Hirata et al.* [2011] and the In Situ Data<sup>a</sup>

|                  | North Central Pacific | Equatorial Pacific | South Pacific |
|------------------|-----------------------|--------------------|---------------|
| Diatoms          | −3.06 (3)             | −8.00 (21)         | −7.00 (7)     |
| Chlorophytes     | −12.35 (2)            | −8.80 (17)         | −38.43 (7)    |
| Cyanobacteria    | −8.12 (24)            | 2.88 (20)          | 0.19 (2)      |
| Coccolithophores | 8.31 (3)              | 17.68 (15)         | 2.53 (7)      |

<sup>a</sup>The number of observations used for the comparison is given in parentheses.

approach was in high latitude and eastern boundary regions where the concentration of microplankton and diatoms were associated with a >35% uncertainty. The uncertainty in the subtropical gyres of the South Pacific was approximately −8% for picoplankton. While the uncertainty for chlorophytes was rather small (<5%), a relatively large uncertainty was found for coccolithophores in tropical oceans [*Hirata et al.*, 2011].

[23] In the Equatorial Pacific, the temporal variation in phytoplankton composition between the two methods was strikingly different. The NOBM suggested a phytoplankton community shift associated with changes in MEI, with diatom and cyanobacteria absolute abundances inversely correlated in response to ENSO events. In contrast, the satellite-derived absolute concentration of all phytoplankton groups were negatively ( $p < 0.05$ ) correlated with the MEI in this region (Table 4). During El Niño events, the satellite-derived absolute concentration of all phytoplankton groups decreased. In fact, all phytoplankton groups were positively correlated with each other in all three regions except cyanobacteria with diatoms in the South Pacific. This was because the satellite-derived approach assumed that changes in phytoplankton composition cannot occur independently of changes in chlorophyll. However, when using relative abundances the shift of

phytoplankton composition in the Equatorial Pacific that was observed with the NOBM was also observed for the satellite-derived approach. In the Equatorial Pacific, the MEI was negatively ( $p < 0.05$ ) correlated to the satellite-derived relative abundance of diatoms ( $r = -0.49$ ) and chlorophytes ( $r = -0.23$ ) and positively correlated to the relative abundance of cyanobacteria ( $r = 0.62$ ) and coccolithophores ( $r = 0.62$ ).

#### 4. Concluding Remarks

[24] These results provide a first line of evidence on how climate variability affects the phytoplankton community structure at a basin scale in the tropical and sub-tropical Pacific Ocean. The results here on the extent of the ocean biology response to climate variability (interannual variability) may have implications for climate change (long-term trends), considering recent results that the intensity and frequency of ENSO events may have increased in past warm periods [*Scroton et al.*, 2011]. This suggests that the overall increase in cyanobacteria concentration and the decrease in the area where diatoms predominate during El Niño events may contribute to the decrease in fish stock and the collapse of fisheries such as the anchovies fisheries that was observed during the 1997–98 El Niño event [*Chavez et al.*, 2003]. Our results suggest that this change in the phytoplankton communities during El Niño events does not occur over the entire Pacific Ocean but rather mostly in the Equatorial Pacific, locally in the North Central Pacific, and has negligible effect on the phytoplankton composition in the South Pacific. We have expended much effort in validation of the large scale distributions of the phytoplankton groups, and have additionally assimilated the total chlorophyll data to improve the realism. We recognize that the results are ultimately dependent upon the physical and physiological characterization of the phytoplankton embedded in the model. While direct observations of phytoplankton composition

**Table 4.** Correlation Coefficient for the Climate Index and Biological Data in North Central Pacific Ocean, Equatorial Pacific and South Pacific Ocean Using the Method of *Hirata et al.* [2011]<sup>a</sup>

|                              | MEI          | Diatoms     | Chlorophytes | Cyanobacteria | Coccolithophores |
|------------------------------|--------------|-------------|--------------|---------------|------------------|
| <i>North Central Pacific</i> |              |             |              |               |                  |
| MEI                          | 1.00         |             |              |               |                  |
| Diatom                       | <b>−0.48</b> | 1.00        |              |               |                  |
| Chlorophytes                 | <b>−0.34</b> | <b>0.48</b> | 1.00         |               |                  |
| Cyanobacteria                | <b>−0.44</b> | <b>0.56</b> | <b>0.51</b>  | 1.00          |                  |
| Coccolithophores             | <b>−0.38</b> | <b>0.67</b> | <b>0.65</b>  | <b>0.63</b>   | 1.00             |
| <i>Equatorial Pacific</i>    |              |             |              |               |                  |
|                              | MEI          | Diatoms     | Chlorophytes | Cyanobacteria | Coccolithophores |
| MEI                          | 1.00         |             |              |               |                  |
| Diatom                       | <b>−0.66</b> | 1.00        |              |               |                  |
| Chlorophytes                 | <b>−0.77</b> | <b>0.60</b> | 1.00         |               |                  |
| Cyanobacteria                | <b>−0.76</b> | <b>0.70</b> | <b>0.72</b>  | 1.00          |                  |
| Coccolithophores             | <b>−0.88</b> | <b>0.71</b> | <b>0.84</b>  | <b>0.86</b>   | 1.00             |
| <i>South Pacific</i>         |              |             |              |               |                  |
|                              | MEI          | Diatoms     | Chlorophytes | Cyanobacteria | Coccolithophores |
| MEI                          | 1.00         |             |              |               |                  |
| Diatom                       | −0.04        | 1.00        |              |               |                  |
| Chlorophytes                 | 0.11         | 0.30        | 1.00         |               |                  |
| Cyanobacteria                | −0.08        | 0.19        | <b>0.63</b>  | 1.00          |                  |
| Coccolithophores             | 0.09         | <b>0.55</b> | <b>0.48</b>  | <b>0.57</b>   | 1.00             |

<sup>a</sup>Bold indicates  $p < 0.05$ .

during ENSO shifts are rare, it is encouraging that those that do exist generally support our results.

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